Multiscale patterns of movement in fragmented landscapes and consequences on demography of the snail kite in Florida

JULIEN MARTIN, JAMES D. NICHOLS*, WILEY M. KITCHENS and JAMES E. HINES*

*Florida Cooperative Fish and Wildlife Research Unit, University of Florida, Gainesville, FL 32611-0485, USA; and *USGS Biological Resources Division, Patuxent Wildlife Research Center, Laurel, MD 20708, USA*

Summary

1. Habitat loss and fragmentation are major factors affecting vertebrate populations. A major effect of these habitat alterations is that they reduce movement of organisms. Despite the accepted importance of movement in driving the dynamics of many natural populations, movement of vertebrates in fragmented landscapes have seldom been estimated with robust statistical methods.

2. We estimated movement probabilities of snail kites *Rosthramus sociabilis* within the remaining wetlands in Florida. Using both radio-telemetry and banding information, we used a multistate modelling approach to estimate transition probabilities at two temporal scales (month; year) and multiple spatial scales. We examined kite movement among wetlands altered by three different levels of fragmentation: among wetlands separated by small physical barriers (e.g. road); among wetlands separated by moderate amount of matrix (< 5 km); and among wetlands separated by extensive matrix areas (> 15 km).

3. Kites moved extensively among contiguous wetlands (movement probability 0·29 per month), but significantly less among isolated wetlands (movement probability 0·10 per month).

4. Kites showed high levels of annual site fidelity to most isolated wetlands (probability ranged from 0·72 to 0·95 per year).

5. We tested the effects of patch size and interpatch distance on movement. Our modelling indicated an effect of both distance and patch size on juveniles' movement (but not adult) when examining movements among fragments.

6. Only a small proportion of kites escaped a regional drought by moving to refugia (wetlands less affected by drought). Many individuals died after the drought. During drought adult survival dropped by 16% while juvenile survival dropped by 86% (possibly because juveniles were less likely to reach refugia).

7. We hypothesize that fragmentation may decrease kite's resistance to drought by restricting exploratory behaviour.

Key-words: capture–recapture models, radio-telemetry, spatially structured population, survival.

Introduction

Habitat loss and fragmentation are major factors affecting populations of many organisms (Holt &

Correspondence: Julien Martin, Florida Cooperative Fish and Wildlife Research Unit, University of Florida, Gainesville, FL 32611-0485, USA. E-mail: martinj@wec.ufl.edu

Debinski 2003). One detrimental effect is reduced movement of these organisms (Smith & Hellmann 2002; Holt & Debinski 2003). This may have important population consequences given that movement is a fundamental process driving the dynamics of fragmented populations, as it connects local populations through emigration and immigration (Hanski 1999; Clobert *et al*. 2001).

To assess how movement influences the dynamics of spatially structured populations, we need to understand how animals perceive, move through, and learn about the landscapes they occupy (Hanski 2001). We also need to evaluate the relative importance of critical factors governing movement processes at pertinent spatio-temporal scales. Patch size, distance between patches, and patch quality are major factors influencing the movement of many animal populations in spatially structured systems (Hanski 1999). Several studies have demonstrated the effect of distance on movement (e.g. Haddad 1999; Hanski 2001). Theoretical models of metapopulation dynamics commonly assume greater emigration from smaller patches (Hanski 2001; Schtickzelle & Baguette 2003), and higher immigration toward larger habitat patches because of the more frequent encounters of moving animals with patch boundaries (**patch boundary effect**) (Lomolino 1990; Hanski 2001).

Fragmentation and habitat reduction reduce patch size and increase the linear distance between patches: both alterations are likely to decrease movement (Holt & Debinski 2003). Creating areas unsuitable for foraging or breeding (i.e. **matrix**) between or around habitats may also decrease survival (Schtickzelle & Baguette 2003).

Despite the importance of providing robust quantitative demographic and movement estimates of populations inhabiting fragmented landscapes (Hanski 2001; Williams, Nichols & Conroy 2002), few empirical estimates exist, especially for vertebrates using large landscapes.

From 1992 to 2004, we studied an isolated population of snail kites *Rosthramus sociabilis* restricted to Florida. The snail kite is a raptor that feeds almost exclusively on freshwater apple snails *Pomacea paludosa* (Beissinger 1988). The kite's restricted diet makes it a wetland-dependent species. As wetlands in Florida have been severely reduced (Davis & Ogden 1994; Kitchens, Bennetts & DeAngelis 2002) since the early 1930s, the population is now confined to the remaining fragments of wetlands extending from the southern end to the centre of the state (Fig. 1).

Because the availability of apple snails to kites is related to hydrologic conditions, variations in water levels are likely to influence snail kite behaviour and demography. In particular, snail availability to kites is greatly reduced during droughts (Beissinger 1995). Beissinger (1986) and DeAngelis & White (1994) described the hydrologic environment used by kites as highly spatially temporally variable. In such a variable environment, one might expect kites to show nomadic tendencies (Bennetts & Kitchens 2000). Bennetts & Kitchens (2000) developed a conceptual model of kite movement along a food resource gradient. They hypothesized that when food is scarce (during drought), kites move to refugia habitats or die. When food is abundant exploratory movements can be done at minimum risk of starvation. During droughts, kites that
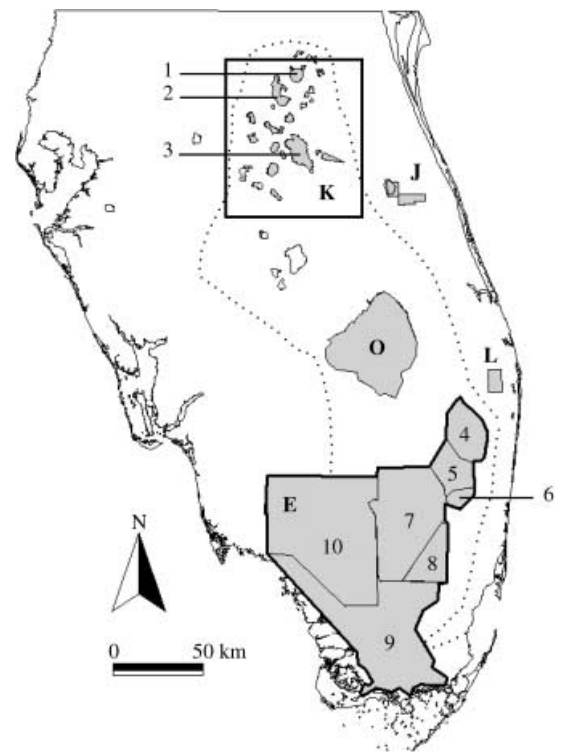
Fig. 1. Major wetlands used by the snail kite in Florida. Regions: Kissimmee Chain of Lakes (K), Everglades (E), Lake Okeechobee (O), Saint Johns Marsh (J), and Loxahatchee Slough (L). Moderately isolated wetlands included in K are: East Lake Tohopekaliga (1), Lake Tohopekaliga (2), Lake Kissimmee (3), as well as the small lakes coloured in grey within the rectangle. Contiguous wetlands included in E: Water Conservation Areas 1A (4), 2A (5), 2B (6), 3A (7), 3B (8), Everglades National Park (9), and Big Cypress National Preserve (10). The grey colouring of the wetlands indicates the area of the wetlands that were included in this study. The thick contour lines delimit regions that include several wetlands. The dotted line indicates the historic Kissimmee–Okeechobee–Everglades watershed that constituted a network of well connected wetlands (Davis & Ogden 1994; Light & Dineen 1994).

have previously explored wetlands throughout their range are less likely to search randomly for alternative habitats, and thus are less likely to starve. Their model also suggests that when food is superabundant, occasional territorial defence may occur for short periods of time, but otherwise kites are typically nonterritorial (Beissinger 1995). Bennetts & Kitchens (2000) estimated the average probability of movement among wetland units (Fig. 1) to be approximately 0·25 per month, which they associated with a nomadic type of behaviour. However, this probability was obtained without considering the complexity of the spatial configuration of the system.

We attempted to enhance our understanding of how kites perceive and move throughout the landscape by incorporating a detailed level of spatial complexity into a modelling approach at multiple spatial scales. First, we estimated movement within a group of **contiguous wetlands** (separated by small physical barriers, easily crossed by kites: such as a road). The distance between

centroids of these contiguous wetlands varied between 16 and 110 km. Second, we estimated movement within a group of wetlands separated by a moderate extent of matrix (< 5 km): **moderately isolated wetlands**. Matrix areas generally consist of nonwetland areas (e.g. agricultural or urban areas). The distance between centroids of these moderately isolated wetlands varied between 10 and 44 km. Third, we estimated movement among wetlands or groups of wetlands isolated by extensive matrix (> 15 km): **isolated wetlands**. To be consistent with the classification of Bennetts *et al.* 1999, we called theses isolated wetlands: **regions**. Most regions used to be connected through the Kissimmee–Okeechobee–Everglades watershed, and became isolated as a result of habitat reduction (Davis & Ogden 1994; Light & Dineen 1994) (Fig. 1). The distance between centroids of these regions varied between 69 and 232 km.

We also explored movement at two temporal scales. First, we examined movement at an annual scale. Because of the period of sampling (i.e. peak of breeding season), this informed us about patterns of breeding and natal philopatry of snail kites. Second, we examined movement patterns on a monthly scale. This period of sampling included the entire year (i.e. including periods outside the breeding season). Thus this study also informed us about movement patterns that were independent of breeding activities (e.g. exploratory movement). Finally, we discussed the consequences of kite movement on survival.

To date, the assumption has been that during a drought, kites move from areas most affected by drought toward areas least affected by drought (Beissinger & Takekawa 1983; Takekawa & Beissinger 1989; Bennetts & Kitchens 2000); and that the impact of a drought on the kite population will depend on the spatial extent and intensity of the drought (Beissinger 1995; Bennetts & Kitchens 2000). However, all hypotheses regarding kite responses to drought are based on count data that do not consider detection probabilities. Therefore, these hypotheses have yet to be rigorously tested and quantified with appropriate statistical methodologies (Williams *et al*. 2002).

HYPOTHESES AND PREDICTIONS

Prediction 1: effect of fragmentation on movement
We predict that movement will covary positively with **connectivity** (i.e. amount of matrix between wetlands). Thus, movement among contiguous wetlands should be greater than among moderately isolated wetlands, and movement among moderately isolated wetlands should be greater than among isolated wetlands (i.e. regions). Prediction 1 implies that movement within regions will be greater than between regions, which could also be explained by a distance effect on movement. However, if movement among contiguous wetlands is greater than among moderately isolated wetlands, the effects of connectivity on movement can be separated from the effects of distance (between centroids), as distances between centroids of contiguous wetlands are

greater than that of moderately isolated wetlands in the study area.

Prediction 2: effect of patch configuration on movement
We expect patch size and distance between patch centroids to influence movement. Movement among patches (i.e. wetlands) should decrease with distance (Hanski 1999). Emigration should be higher from smaller patches (Hanski 2001; Schtickzelle & Baguette 2003), and immigration should be higher toward larger patches (Lomolino 1990; Hanski 2001).

Prediction 3: patch configuration affects juvenile movement more than adult movement
Patch size and distance between patches are more likely to influence movement of birds that have never dispersed from their natal area (typically young individuals), than birds that are aware of wetlands outside their natal area. Because we expect the number of wetlands visited to increase with time, on average juveniles (≤ 1 year) should have visited fewer wetlands than adults. Therefore, movement of juveniles should be less influenced by habitat characteristics (e.g. habitat quality) of destination sites than movement of adults, whose movement may be partly influenced by their knowledge of the location of multiple wetlands (assuming that kites remember sites they have already visited). This prediction is derived from hypotheses developed by Bennetts & Kitchens (2000) and Bell (1991), who suggested that many species learn from exploratory movements, and thus modify their movement patterns according to their experience with visited habitats. Thus we expect a stronger relationship between movement and geometric features of the landscapes for juveniles than for adults.

Prediction 4: drought effect on movement
a During a drought, we predict that some birds will move from areas most affected to areas least affected by drought (e.g. Takekawa & Beissinger 1989).
b Because of their knowledge of alternative wetlands and the paths linking these wetlands, adult birds should be more successful than juveniles in moving to refugia habitats.

Prediction 5: drought effect on survival
a As predicted by Beissinger (1995) and Bennetts & Kitchens (2000), we expect survival to be lower during drought.
b Survival should be lower in regions most affected by drought.
c Because adults are more likely to move successfully to areas least affected by drought, we expect survival to decrease more for juveniles than for adults.

Methods

STUDY AREA

This study was conducted throughout South & central Florida, encompassing most of the habitats used by

© 2006 The Authors.
Journal compilation
© 2006 British
Ecological Society,
*Journal of Animal
Ecology*, **75**,
527–539

the snail kite. Thirteen wetlands were sampled (Fig. 1). Given that kites can cross small physical barriers delimiting each wetland (e.g. road) with relative ease (Bennetts 1998), we further aggregated the units into five larger groups of wetlands (regions) (Fig. 1). We used Bennetts (1998) and Bennetts *et al.* (1999) definition of a region. Regions were separated from other regions by an extended matrix (> 15 km). Water Conservation Areas (WCAs), Everglades National Park and Big Cypress National Preserve constituted a group of contiguous wetlands and were grouped into one region: the Everglades region (E). The Kissimmee Chain of Lakes region (K) included Lake Tohopeka-liga, East Lake Tohopekaliga, Lake Kissimmee, and all the small lakes in the surrounding areas. Wetlands in the K region were isolated by moderate extent of matrix (< 5 km). Lake Okeechobee (O), St Johns Marsh (J), and Loxahatchee Slough (L), constituted their own regions. Areas of wetlands and distances between wetlands were estimated using a Geographic Information System (ArcView GIS 3·2; Xtools, DeLaune 2000).

CRITERIA FOR DETERMINING THE REGIONAL IMPACT OF THE 2001 DROUGHT

We used water-stage data (elevation of water surface measured in feet above the National Geodetic Datum of 1929) recorded daily in each of the major wetland units and made available by the South Florida Water Management District (http://www.sfwmd.gov/org/ema/dbhydro) to develop an index of drought impact. We used the data corresponding to the period of study (1992–2003). Water stage was averaged by month for the entire time series. We calculated the mean of the monthly average stages for March through June of each year. This period is especially critical for apple snail breeding and availability to the kites (Darby 1998) and also includes the greater part of the seasonal dry season when water stages are at their annual minimum (i.e. when water levels are most likely to affect kite survival and movement).

We determined the mean stage for the period of record (1992–2003) for each major wetland unit and determined where drought-year water stage means fell in terms of standard deviations below this value. This method, proposed by Bennetts (1998), allows for comparisons of drought intensity among wetlands for the period of record. The 2001 drought occurred between January and August (Smith *et al.* 2003). Intensity of drought was maximal for the lowest drought score values (DSV). Bennetts (1998) considered wetlands to be under drought conditions whenever DSV < −1. This analysis indicated that region E (WCA3B DSV = −2·32; Big Cypress DSV = −2·28; WCA1A DSV = −2·18; WCA3A DSV = −1·92; WC2B DSV = −1·41; WCA2A DSV = −1·20) and region O (DSV = −2·57) were the most impacted, while region K (Lake Kissimmee DSV = −0·72; Lake Tohopekaliga DSV =

−0·84; Lake East Toho DSV = −0·98) was the least affected. Region J was also affected (DSV = −1·92).

STATISTICAL MODELS TO ESTIMATE MOVEMENT AND SURVIVAL

Multistate capture–recapture models (Hestbeck, Nichols & Malecki 1991; Williams *et al.* 2002) were used to estimate apparent survival (ϕ), movement probabilities (ψ) and detection probabilities (p) simultaneously. ϕ^u was defined as the probability for a kite alive in location u (i.e. wetland u) at time t to survive between time t and $t + 1$; and p^u was the probability of detecting (sighting) a kite that was alive and associated with wetland u. We defined ψ^{us} as the probability that a kite in wetland u at time t was in wetland s at time $t + 1$, given that it was alive at $t + 1$. Modelled parameters used notation from Senar, Conroy & Borras (2002); time dependency was (t) and no time effect was ($\cdot$). We assigned each bird to one of two age classes: juveniles (*juv*), 30 days to 1 year; and adults (*ad*), older than 1 year. Effects embedded in other factors are shown using parentheses. A multiplicative effect is shown by (*) and an additive effect is shown by (+). All computations of the movement and survival probabilities were carried out using program MARK V 4·1 (White & Burnham 1999).

FIELD METHODS FOR THE STUDY OF MOVEMENT ON A MONTHLY SCALE

Between 1992 and 1995, 165 adult and 120 juvenile snail kites were equipped with radio transmitters with a battery life of approximately 9–18 months (Bennetts & Kitchens 2000). Between 1992 and 1995, aircraft radio-telemetry surveys were conducted on a weekly basis (two 4–5 h flights every week) over a large portion of the entire range of the population in Florida. Previous analyses by Bennetts *et al.* (1999) and Bennetts (1998) found no evidence of radio effects on survival or movement probabilities.

STATISTICAL METHODS TO ESTIMATE MOVEMENT ON MONTHLY SCALE USING RADIOTELEMETRY

Estimating monthly movement among regions
To estimate monthly movement probabilities (ψ) of radio-tagged individuals among regions, we used multistate models. Because monthly survival estimates were beyond the scope of our study, we removed individuals from the analysis after they were last observed and fixed survival parameters to 1. For this analysis, we included individuals for which the fate and location could be determined with certainty (i.e. detection probability equals 1). In addition, birds that temporarily disappeared and then reappeared in the sample were censored when they disappeared and were included again when they reappeared (Williams *et al.* 2002).

This analysis included six states: the five regions described above (E, K, O, L, J) (Fig. 1), and one state containing peripheral habitats and matrix area (P, all locations outside the sampled areas). To compute the probability of movement out of a patch (wetland or region), we summed the transition probabilities out of that patch. To calculate the **average monthly probability** of movement out of any wetland within a region, we computed the average of the monthly movement probabilities out of every wetland in the region of interest.

We tested the effect of patch size (AR for the surface area of the receiving site, and AD for the surface area of the donor site), distance (d), region (r), age, and time on movement probabilities. The notations for age and time followed the ones common to all analyses. We also tested the effect of year (*year*), given that the radio-telemetry study was conducted between 1992 and 1995. A seasonal effect (*seas*) with respect to three 4-month seasons (January–April, May–August, September–December) (Bennetts & Kitchens 2000); and a breeding season effect (*breed*; breeding season: January–June; nonbreeding season: July–December) were also included.

With known fate multistate data (for which the detection probability is 1), there is currently no appropriate **Goodness of Fit test (GOF)**. However, most analyses presented in our study included fairly general models.

Estimating monthly movement within regions using radio-telemetry

The same method was used for this analysis as for the among-regions analysis. Because two regions comprised several wetland units, we conducted two separate analyses. The analysis for the K region contained four moderately isolated wetlands (denoted: *mw*): Lake Tohopekaliga, Lake East Tohopekaliga, Lake Kissimmee, and a site containing all of the small lakes in the surrounding area (Fig. 1). Analysis for the Everglades region contained five contiguous wetlands (denoted: *cw*): WCA3A, WCA3B, Everglades National Park and Big Cypress (Fig. 1). We also, aggregated three contiguous wetlands (WCA1, WCA2A and WCA2B), into one site, as our data set would not have permitted a seven-site model. Patch size and distance were included as factors in the models of region E only. This analysis was not applicable for region K, because of the site that included all of the small lakes.

FIELD METHODS FOR THE STUDY OF MOVEMENT AND SURVIVAL ON A ANNUAL SCALE

We used mark–resighting information collected during the peak of the breeding season (March 1–May 30), for a period of 13 years (1992–2004). Between 1992 and 2004, 1730 juveniles were marked just before fledging. Juveniles advance to the adult age class at the beginning of the next breeding season (Bennetts, Kitchens & Dreitz 2002). In addition, between 1992 and 1995, 134 adults (i.e. older than 1 year) were banded. Bands were uniquely numbered anodized aluminium colour bands. Banded kites were identified from a distance, using a spotting scope. Each wetland was surveyed at least once using an airboat.

STATISTICAL METHODS TO ESTIMATE ANNUAL MOVEMENT AND SURVIVAL USING BANDING DATA

We used a multistate model to estimate annual movement and survival probabilities. We assigned the location of each bird to four regions (see Study area). We excluded region L from this analysis to maximize precision, as relatively few birds were recorded in this area.

Estimating survival

A set of biologically relevant models was developed that allowed ϕ and p to vary across time, or stay constant for each age class. Because our data set included kites banded as juveniles and as adults, age was modelled both as time since marking and as a group effect. We also created models that included drought effect on ϕ and p. We included a drought effect, which assumed different effects on apparent survival in 2000–01 and 2001–02 (denoted: D_{1-2}). We used this approach because the drought was likely to affect ϕ before and after the 2001 sampling occasion. ND indicated that ϕ was constant during the remaining nondrought years (denoted: ND). For juveniles we designed models with additive effect of time and region ($t + r$) on ϕ, but because of the drought few juveniles were fledged in 2001 (32 juveniles were fledged in K, three in J and none in E and O). We thus constructed models with additive effect of time and region on ϕ, except during the interval 2001–02, during which ϕ was assumed to be similar among regions (denoted: $\phi_{juv}(r + t_d)$). Consequently, during the interval 2001–02 model $\phi_{juv}(r + t_d)$ reflected apparent survival for northern regions (K and J). Because we expect environmental conditions to be more similar among neighbouring regions than among regions that are far apart, we expect survival in regions close to each other, to be similar. Thus we developed models that assumed similar apparent survival probabilities in neighbouring regions. Owing to the proximity of regions E and O in the south (separated by 30 km) and K and J in the north (separated by 25 km) (conversely, O and J were separated by 50 km; Fig. 1), we developed models with a common survival parameter for each group of regions (denoted $\phi^{[E=O\neq K=J]}$; superscripts indicate regions the survival probabilities pertain to; '=' indicates that ϕ^E is the same as ϕ^O, similarly ϕ^K is the same as ϕ^J; '$\neq$' indicates that ϕ^E and ϕ^O are different from ϕ^K and ϕ^J). Models assuming a different ϕ for each region were denoted ($\phi(r)$).

Because the drought intensity was strongest in E, O and J (lowest DSV), and weakest in K (highest DSV), some models assumed similar drought effects on ϕ in E,

O and J (denoted $\phi^{[E=O=J]}$ (D_{1-2})); with no drought effect on ϕ in K ($\phi^K(\cdot)$).

Estimating annual movement probabilities among regions using banding data

Our multistate approach using the banding data (described above) provided annual estimates of movement probabilities (ψ), among four regions (E, O, K and J). We tested the effect of the drought on movement between 2000 and 2001 (denoted D_1). We also estimated the probability for a kite to be found in a particular region (u) at year $t + 1$, given that it was present in that same region in year t (ψ^{uu}). These probability estimates were used to evaluate the level of philopatry at each site. These estimates were obtained as one minus the estimated probabilities of moving away from the area.

Goodness of fit

Previous survival analyses indicated a strong age effect on ϕ (Bennetts *et al*. 2002). Unfortunately, we are not aware of GOF test accounting for an age effect on ϕ for multistate model. However, it is possible to test the fit of adult data separately. We used program U-CARE version 2·02, which tests the fit of the 'Jolly move' (JMV) and Arnason–Schwarz models (AS) (Pradel, Wintrebert & Gimenez 2003). We were only able to test model JMV, which fit the data satisfactorily when testing the fit of adult data separately ($x^2_{102} = 104\cdot3$, $P = 0\cdot42$). The fit of the JMV model could not be assessed on juveniles separately (Test M requires > 4 occasions). Thus, as suggested by Senar *et al*. (2002) we computed a GOF accounting for an age effect (by summing Test 3.SM, Test 2.CT and Test 2.CL, available from program U-CARE, see Choquet *et al*. 2003), for a site-specific Cormack–Jolly–Seber (CJS) model in lieu of a multistate model. The site-specific CJS model fitted the data satisfactorily ($x^2_{175} = 152\cdot1$, $P = 0\cdot89$). We concluded that there was no evidence of lack of fit of the multistate model used (i.e. models in Table 3 accounted for an age effect on ϕ; Choquet *et al*. 2003).

MODEL-SELECTION PROCEDURE

For each mark–resight analysis, we first developed and fitted a set of biologically relevant models that corresponded to our best a priori hypotheses (referred as starting models). We then developed models whose relevance was linked to the need to evaluate the fit of each of the starting models (Cam, Oro & Jimenez 2004). We used AICc (Burnham & Anderson 2002) as a criterion to select the model that provided the most parsimonious description of the variation in the data (i.e. model with the lowest AICc). The value of ΔAICc (the difference between the AICc of a particular model and that of the model with the lowest AICc) was presented in each set of model-selection results. We also used AICc weight (*w*) as a measure of relative support for each model (Burnham & Anderson 2002). We reported only the model whose *w* was greater than 0·01.

EFFECT OF PATCH SIZE AND DISTANCE ON MOVEMENT

Movement probabilities were modelled as linear-logistic function of patch size and/or distance (Blums *et al*. 2003). For example, probabilities of moving from one patch to another in function of distance were modelled as:

$$\text{Logit}(\psi(d)) = \beta_i + \beta_d(d),$$

where β_i, β_d, are the parameters to be estimated. β_i is the intercept, β_d is the slope for distance between patch centroids (d). Probability of moving was predicted to decrease with increasing distance between patches ($\beta_d < 0$) (Blums *et al*. 2003). Whenever the 95% CI [$\hat{\beta}_d$] estimate did not overlap 0, the relation was considered statistically significant.

EFFECT SIZE

To measure the magnitude of the difference between estimates we computed estimates of 'effect size' ($\widehat{ES}$) as the arithmetic difference between estimates. Whenever the 95%CI [$\widehat{ES}$] did not include 0 the difference was considered statistically significant (Cooch & White 2005).

ESTIMATES OF PRECISION

Variances for derived estimates in our study were computed using the delta method (Williams *et al*. 2002). Confidence intervals for estimates that were strictly positive (ϕ, ψ), were computed using the method proposed by Burnham *et al*. (1987) based on the log-normal distribution (Appendix S1 in Supplementary material).

Estimates of effect size (not strictly positive), were approximated as follows: 95%CI [$\hat{\theta}$] = $\hat{\theta} \pm 1\cdot96 * \widehat{SE}$ [$\hat{\theta}$].

Results

MONTHLY MOVEMENT PROBABILITIES AMONG REGIONS

Effects of patch size and distance

The most parsimonious model (with lowest AICc; Table 1a), was a model that only included a site-specific effect of movement ($\psi(r)\cdot$). However, the model that assumed movement probabilities to be site-specific for adults, but included a patch-size and a distance-between-patches effect plus interaction of these factors for juveniles ($\psi_{ad}(r)\psi_{juv}(AR*d)$), also received some support (ΔAICc = 1·7; Table 1a). This model had considerably more support than the model that assumed movement probabilities to be solely site-specific for adult birds and juveniles ($\psi_{ad}(r)\psi_{juv}(r)$; ΔAICc = 15·2; see also Table S2a in Supplementary material).

When the analysis is conducted on juveniles only, the model $\psi_{juv}(AR*d)\cdot$ is considerably better than $\psi_{juv}(r)$

Table 1. Multistate models (with survival and detection probabilities equal to 1) of monthly movement probabilities (ψ) of adult (*ad*) and juvenile (*juv*) snail kites among the five major regions (E, O, K, L, J) and P (peripheral and matrix areas), based on radio-telemetry data. These models evaluate the effect of patch size, distance and regional identity alone on movement probabilities

Model	ΔAICc	*w*	K
(a) Movement among regions of juveniles and adults modelled simultaneously			
$\psi(r)$	0	0·69	30
$\psi_{ad}(r)\,\psi_{juv}(AR*d)$	1·7	0·30	43
$\psi_{ad}(r)\,\psi_{juv}(AD)$	8·2	0·01	40
(b) Movement among regions modelled using data from juveniles only			
$\psi_{juv}(AR*d)$	0	0·79	13
$\psi_{juv}(AR+d)$	3·0	0·17	12
$\psi_{juv}(AD)$	6·5	0·03	10
$\psi_{juv}(AR)$	8·8	0·01	11
(c) Movement among regions modelled using data from adults only			
$\psi_{ad}(r)$	0	1·00	30

Notes: AICc is the Akaike's Information Criterion. ΔAICc for the ith model is computed as $AICc_i - \min(AICc)$. *w* refers to AICc weight. K refers to the number of parameters. Only models with *w* > 0·01 are presented (see Table S2 in Supplementary material, for models with *w* < 0·01).
'*r*': region (includes six states: E, O, K, J, L and P (peripheral and matrix); '*AR*': Area of the receiving site; '*AD*': Area of the donor site; '*d*': distance.

Table 2. Multistate models (with survival and detection probabilities equal to 1) of monthly movement probabilities (ψ) of adult (*ad*) and juvenile (*juv*) snail kites among wetlands in the E and K region based on radio-telemetry data. These models evaluate the effect of patch size, distance, season, and wetland identity alone on movement probabilities

Model	ΔAICc	*w*	K
(a) Movement within the E region of adult and juvenile snail kites			
$\psi(seas*cw)$	0	1	20
(b) Movement within the K region of adult and juvenile snail kites			
$\psi(seas)$	0	0·67	3
$\psi_{ad}(seas)\,\psi_{juv}(seas)$	2·6	0·18	6
$\psi(\cdot)$	5·4	0·04	1
$\psi_{ad}(\cdot)\,\psi_{juv}(\cdot)$	6·5	0·03	2
$\psi(mw)$	6·5	0·03	12
$\psi(breed)$	7	0·02	2
$\psi(years*seas)$	8	0·01	10

Notes: Only models with *w* > 0·01 are presented (see Table S3 in Supplementary material, for models with *w* < 0·01).
'*cw*': contiguous wetland; '*mw*': moderately isolated wetland; '*seas*': season; '*breed*': breeding season. For other notations see Table 1.

(ΔAICc = 14; Table 1b; see also Table S2b in Supplementary material), indicating that patch size and distance may be important in determining the movement probabilities of juveniles. Model $\psi_{juv}(AR*d)$ indicates that the probability of moving between two locations decreased with distance between these locations ($\hat{\beta}_d = -0\cdot020$, 95%CI = $-0\cdot032$ to $-0\cdot007$). Conversely, we could not show any relationship between the receiving site area and movement with this model ($\hat{\beta}_{AR} = -0\cdot020$, 95% CI = $-0\cdot247–0\cdot207$). The interaction for this model was positive, but not very strong ($\hat{\beta}_{AR*d} = 0\cdot002$, 95%CI = $0\cdot0001–0\cdot003$). We also tried a model with an additive effect of distance and patch size of the receiving sites, $\psi_{ad}(r)\psi_{juv}(AR+d)$. That model did not reach numerical convergence with program MARK when the data set included both juvenile and adult birds; we consequently ran this model on a data set that only comprised juvenile birds [$\psi_{juv}(AR+d)$; Table 1b]. Although this model was less parsimonious than one that incorporated an interaction effect (ΔAICc = 3; Table 1b), it was considerably better than the site-specific model (ΔAICc = 14; see also Table S2b in Supplementary material). Model $\psi_{juv}(AR+d)$ supported the hypothesis of a negative relationship between movement probabilities and distance ($\hat{\beta}_d = -0\cdot011$, 95%CI = $-0\cdot020$ to $-0\cdot0030$). This model also supported the hypothesis of a positive relationship between movement and size of the receiving sites

($\hat{\beta}_{AR} = 0\cdot205$, 95%CI = $0\cdot120–0\cdot289$). The models that included the size effect of the donor patch on juvenile movement $\psi_{juv}(AD)$ received little support (ΔAICc = 6·5; Table 1b), but the β parameter for *AD* supported the hypothesis that emigration was lower out of larger patches ($\hat{\beta}_{AD} = -0\cdot191$, 95%CI = $-0\cdot298$ to $-0\cdot084$).

There was no evidence of any patch size or distance effect on adult movement (Table 1a,c). Models that included effects of time, year, or season received no support (*w* ~ 0).

MONTHLY MOVEMENT PROBABILITIES WITHIN REGIONS

Movement within the Everglades region
The most parsimonious model for this analysis was $\psi(seas*cw)$ (*w* ~ 1; Table 2a), which assumed movement probabilities to vary by season and to be site-specific.

Movement within the K region
The most parsimonious model for this analysis assumed movement to vary by season $\psi(seas)$; *w* = 0·67; Table 2b).

COMPARISON AMONG AND WITHIN REGIONS

The probability that a snail kite in any of the five wetlands in region E moved to another unit in that same region within the next month (**average monthly movement probability** among contiguous wetlands), using model $\psi(seas*cw)$ for the Everglades region (Table 2a), was 0·29 (95%CI = 0·24–0·35). By contrast, the monthly movement probabilities from E to the four

other regions was only 0·04 (95%CI = 0·03–0·05), using model $\psi(r)$ (Table 1a). The same pattern was observed in region K where kites moved extensively among the moderately isolated wetlands in this region, using model $\psi(seas)$ (Table 2b) we found the average monthly probability $\hat{\psi} = 0.15$ (95%CI = 0·13–0·17); with only a 0·09 (95%CI = 0·06–0·12) monthly movement probability from this region to the four other regions, using model $\psi(r)$ (Table 1a).

The probability that kites in any of the five regions moved to another region within the next month (average monthly movement among isolated wetlands), using model $\psi(r)$ (Table 1a) was 0·10 (95%CI = 0·08–0·12).

Average monthly movement among contiguous wetlands was significantly greater than among moderately isolated wetlands ($\widehat{ES} = 0.14$, 95%CI = 0·08–0·20). Average monthly movement among moderately isolated wetland was significantly greater than among isolated wetlands ($\widehat{ES} = 0.05$, 95%CI = 0·02–0·07); and average monthly movement among contiguous wetlands was significantly greater than among isolated wetlands ($\widehat{ES} = 0.19$, 95%CI = 0·13–0·25).

INTERANNUAL SURVIVAL ESTIMATES

The most parsimonious model $\phi_{ad}^{[E=O\neq K=J]}(ND)\phi_{ad}^{K}(\cdot)$ $\phi_{ad}^{[E=O=J]}(D_{1-2})\phi_{juv}(r+t_d)p(r*t)\psi(r*D_1)$ received overwhelming support from the data ($w = 0.96$; Table 3). This model had region-specific apparent survival for adults, which did not vary over time but differed significantly between drought and nondrought years (Fig. 2). There was an additive effect of region and time for estimates of apparent survival of juveniles, except for the interval 2001–02, during which ϕ was assumed
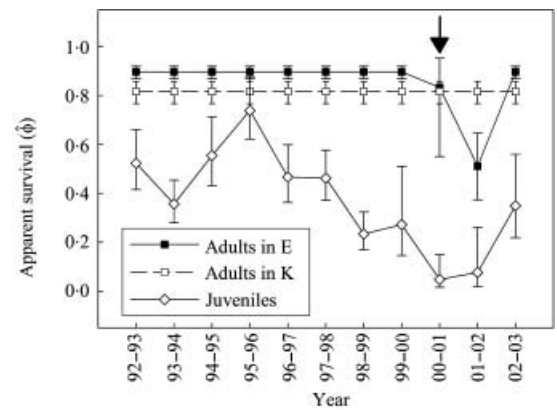

Fig. 2. Apparent survival ($\hat{\phi}$) between 1992 and 2003 of adult and juvenile snail kites, obtained using the most parsimonious model in Table 3. Error bars correspond to 95% confidence intervals. During nondrought years (1992–2000 and 2002–03), $\hat{\phi}$ of adults were similar in E and O; and in K and J. During drought (2000–02), $\hat{\phi}$ of adults were similar in E, O and J, but different in K. For readability, only $\hat{\phi}$ in E and K are presented for adults. $\hat{\phi}$ of juveniles were averaged across regions. Arrow indicates the beginning of the drought that started in January 2001. Estimates between 1992 and 1999 were consistent with Bennetts *et al.* (2002).

to be time-dependent only. Sighting probabilities were region and time specific. Movement probabilities were region specific and were affected by the drought. Apparent survival estimates for adult kites located in neighbouring regions during nondrought were similar (i.e. $\hat{\phi}^{E} = \hat{\phi}^{O}$ and $\hat{\phi}^{J} = \hat{\phi}^{K}$). During nondrought years $\hat{\phi}^{E}$ was greater than $\hat{\phi}^{K}$ (ES = 0·08, 95%CI = 0·03–0·13; Fig. 2). This model also assumed no significant effect of drought on adult apparent survival in K (the region with the highest DSV > −1), but assumed a similar effect of drought on adult apparent survival in E, O and J (which all had lower DSV < −1) (see Fig. 2 for estimates).

Average estimates of juvenile apparent survival during nondrought years were higher in southern regions ($\hat{\phi}^{E} = 0.520$, 95%CI = 0·460–0·588; $\hat{\phi}^{O} = 0.471$, 95%CI = 0·372–0·597) than in northern regions ($\hat{\phi}^{K} = 0.355$, 95%CI = 0·233–0·541; $\hat{\phi}^{J} = 0.412$, 95%CI = 0·295–0·575), but confidence intervals overlapped. During drought years confidence intervals of region specific juvenile apparent survival overlapped widely ($\hat{\phi}^{E} = 0.07$, 95%CI = 0·014–0·349; $\hat{\phi}^{O} = 0.0647$, 95%CI = 0·010–0·427; $\hat{\phi}^{K} = 0.054$, 95%CI = 0·007–0·405; $\hat{\phi}^{J} = 0.058$, 95%CI = 0·004–0·837). Because no juveniles were marked in 2001 in E and only four were marked in K in 2000, we could not test the hypothesis of a lower effect of the drought on apparent survival of juveniles in K. Given that juvenile apparent survival estimates were not significantly different from one another we averaged these estimates across regions (Fig. 2).

Estimates of adult apparent survival averaged across regions remained fairly high and constant over time ($\hat{\phi} = 0.86$; Fig. 2), but dropped substantially during

Table 3. Multistate models of annual apparent survival (ϕ), sighting (p), and movement probabilities (ψ) of adults (*ad*) and juveniles (*juv*) snail kites based on banding data. The drought effect on ϕ during 2000–02 was denoted D_{1-2}. The drought effect on ψ in 2001 was denoted D_1. Constant ϕ during nondrought years (1992–2000 and 2002–04) was denoted *ND*. Because all models included in Table 3 had region- and time-dependent sighting probabilities ($p(r*t)$), Table 3 only includes model structures for ϕ and ψ

Model	ΔAICc	*w*	K
$\phi_{ad}^{[E=O\neq K=J]}(ND)\phi_{ad}^{K}(\cdot)\ \phi_{ad}^{[E=O=J]}(D_{1-2})$ $\phi_{juv}(r+t_d)\psi(r*D_1)$	0	0·96	85
$\phi_{ad}^{[E=O\neq K=J]}(ND)\phi_{ad}^{K}(\cdot)\ \phi_{ad}^{[E=O=J]}(D_{1-2})$ $\phi_{juv}(r+t_d)\psi(r)$	7	0·03	78

Notes: Only models with *w* > 0·01 are presented (see Table S4 in Supplementary material, for models with *w* < 0·01). '*t*': time (years); '$r+t_d$': additive effect of region and time on ϕ, except during 2001–02, during which ϕ was time-dependent only; '·': ϕ is constant during 1992–2004. Superscript indicate region specific ϕ; '=': regions have identical ϕ; '≠': regions have different ϕ. For other notations see Table 1.

drought years between 2000 and 2002 (average apparent survival between 2000 and 2002 was $\hat{\phi} = 0.72$; Fig. 2). This represented a relative decrease of 16% in apparent survival during the years that were affected by the drought when compared with nondrought years, but the decrease was only significant between 2001 and 2002 (ES = 0·39, 95%CI = 0·24–0·53; Fig. 2). Juvenile apparent survival varied widely over time, but reached a record low between 2000 and 2002 (average $\hat{\phi}$ between 2000 and 2002 was $\hat{\phi} = 0.06$; Fig. 2). Juvenile apparent survival decreased by 86% in 2000 and 2002 (relative decrease) when compared with its average over the nondrought years (average $\hat{\phi}$ during 1992–99 and 2002–03 was $\hat{\phi} = 0.44$).

INTERANNUAL MOVEMENT AMONG REGIONS AND DROUGHT EFFECT ON MOVEMENT

The most parsimonious model (described above; Table 3), had site-specific annual transition (movement) probabilities that were constant over time, except during the drought (Table 3). This model was substantially better supported than the same model without a drought effect (ΔAICc = 7; Table 3). Using the most parsimonious model, we found that during the 2001 drought, movement estimates were higher from the areas with the lowest DSV (i.e. most impacted regions: O and E) toward areas with highest DSV (i.e. least impacted region: K), $\hat{\psi}^{OK} = 0.33$ (95%CI = 0·146–0·580), $\hat{\psi}^{EK} = 0.030$ (95%CI = 0·014–0·066), than during nondrought years $\hat{\psi}^{OK} = 0.044$ (95%CI = 0·024–0·080), $\hat{\psi}^{EK} = 0.015$ (95%CI = 0·010–0·025). However, the difference was only statistically significant for birds moving from O to K ($\widehat{ES} = 0.28$, 95%CI = 0·05–0·52). Estimated movement probabilities toward the most-impacted region (i.e. E and O) during the drought approached zero. This contrasted with nondrought years during which movement probabilities toward E and O were typically much higher than zero (ranged from 0·02 to 0·16; Table S5 in Supplementary materials). Surprisingly, the probability of moving from J to K during the drought approached zero, while during nondrought years this probability was $\hat{\psi}^{JK} = 0.06$ (95%CI = 0·03–0·11).

Models including an age effect as well as a drought effect on movement did not reach numerical convergence; however, we did not detect any movement of juvenile bird from the most to the least impacted regions between 2000 and 2001. Models including an age effect on movement but no drought effect were not supported ($w < 0.01$; Table S4 in Supplementary material).

We used the most parsimonious model to estimate the probability of staying in each region from one year to another. The probability of staying in E was $\hat{\psi}^{EE} = 0.95$ (95%CI = 0·94–0·96), the probability of staying in O was $\hat{\psi}^{OO} = 0.76$ (95%CI = 0·71–0·82), the probability of staying in K was $\hat{\psi}^{KK} = 0.72$ (95%CI = 0·66–0·79), and the probability of staying in J was $\hat{\psi}^{JJ} = 0.75$ (95%CI = 0·69–0·82).

Discussion

MONTHLY MOVEMENT AMONG CONTIGUOUS AND ISOLATED WETLANDS

We found that kites moved extensively over large areas of contiguous wetlands (average monthly movement probability: 0·29). However, our study also showed much less movement among isolated wetlands (average monthly movement probability: 0·10). As expected average monthly movement probability among moderately isolated wetlands was intermediate: 0·15. Differences between these estimates were all statistically significant. These results agree with *Prediction 1*, that loss of connectivity reduces movement of kites. However, as stated in *Prediction 1* only by comparing movement among contiguous wetlands and among moderately isolated wetlands could the effect of connectivity and distance be separated. Indeed, despite the fact that distances between the centroids of contiguous wetlands (E) were greater than between the centroids of moderately isolated wetlands (K), movement among wetlands in E were greater than in K. The results also suggest that seasonality influenced movement within, but not among regions. One possible explanation is the pronounced wet–dry seasonality resulting in spatio-temporally variable habitat conditions at both the local and regional levels (Davis & Ogden 1994; Bennetts & Kitchens 2000). The fact that this seasonal pattern was not observed for movements among regions may be due to the higher costs (i.e. mortality) associated with moving among regions than when moving within the regions.

PATCH SIZE AND DISTANCE BETWEEN PATCHES AS FACTORS DRIVING MOVEMENT

Our modelling approach provided supportive evidence that patch size and interpatch distance constitute important factors influencing movement of juveniles at the regional scale. The support for this hypothesis was weak when movement was modelled for juveniles and adults simultaneously (Table 1a). However, this hypothesis received substantially more support when juvenile movement was modelled separately (Table 1b,c). Our results are thus consistent with *Prediction 2*, which predicts that movement probabilities between regions on a monthly scale decrease with distance. The hypothesis that immigration should be higher toward larger patches because of more frequent encounters with patch boundaries (*see Prediction 2*; Lomolino 1990; Hanski 2001) received some limited support. Indeed, model $\psi_{juv} (AR + d)$ (Table 1b) which supported the hypothesis of a positive relationship between movement and the size of the receiving site had a w of 0·17 (Table 1b). Although the model that assumed higher emigration out of smaller areas for juveniles ($\psi_{juv}(AD)$) was not parsimonious (Table 1b), examination of the β parameter for this model supported this hypothesis.

The fact that we only found evidence of a patch size and distance effect on the monthly movement probabilities of the juveniles at the regional scale is consistent with *Prediction 3*. However, we can only infer that juveniles may respond to distance and size of the destination site, whereas adults do not (Table 1c), possibly indicating that adults are responding to other factors (e.g. habitat quality). Only by including a measure of habitat quality (currently unavailable) in our models could we test the hypothesis that adult movements are more likely to be determined by the acquired knowledge of the quality of the available habitats than by the patch boundary effect. The fact that we found no influence of patch size and distance on monthly movement among contiguous or moderately isolated wetlands can be explained by the fact that movements among these wetlands are so frequent that the effect of patch size effect and distance may be diluted over time (i.e. after a few months birds may not search wetlands blindly anymore).

If patch size and distance affect movement patterns among patches, one can see how habitat loss and fragmentation may affect dispersal, particularly for juvenile birds. It is particularly likely to increase the search cost when animals move to locate new suitable wetlands.

INTERANNUAL PATTERN OF MOVEMENT

Despite relatively high average monthly movement probabilities out of regions (e.g. average movement probabilities out of E and K were 0·04 and 0·09, respectively), kites exhibited strong philopatric tendencies to particular regions at an annual scale (e.g. annual estimates of site tenacity for regions E and K were 0·95 and 0·72, respectively).

This extent of site tenacity is surprising given the high environmental variability that characterizes the kite's range in Florida (Beissinger 1986; DeAngelis & White 1994). Indeed many species that use environments where food resources vary strongly in space and time are often nomadic (e.g. DeAngelis & White 1994). However, movement out of familiar areas may incur important search costs (starvation, predation). Kites may also benefit from staying in or returning to familiar regions, as it could contribute to maximizing their breeding output and chance of survival (e.g. predation avoidance) (Stamps 2001).

In summary, kite movement in this fragmented system varies from site tenacity (between breeding season and at the regional scale) to nomadism (within region on a monthly scale), depending on the spatio-temporal scale of observation and hence on the activities of primary relevance at different times and places. In particular, one may want to distinguish between breeding (or natal) philopatry and exploratory movements, as the factors governing these processes may be different. Additionally, our results indicate that snail kites move substantially less between regions that have been isolated by human-induced fragmentation than within these

regions. Thus, many kites may have little familiarity with wetlands located outside their natal region. A regional disturbance could therefore have significant demographic consequences. Kites that are familiar with many landscapes within the population's range may survive a regional drought by moving to other less-affected regions, while survival of birds without knowledge of alternative wetlands could be dramatically reduced. The drought that occurred in Florida in 2001 provided an opportunity to evaluate the effects of this type of natural disturbance on kites.

REGIONAL SURVIVAL AND RESISTANCE OF THE POPULATION TO NATURAL DISTURBANCE

The analysis of annual movement indicates that kite movement was affected by the 2001 drought. As expected, a proportion of birds moved from the most to the least-impacted regions, which is consistent with *Prediction 4a* (but the drought effect was only significant for kites moving from O to K). Although models, including an age effect on annual movement, were not supported (possibly because of low sample size), no juveniles that had fledged 1 year prior to the drought were found to have moved toward refugia (i.e. only adult birds were observed moving to region K in 2001). This latter observation is not based on any robust estimation procedure and therefore should be interpreted with caution. However, it is worth pointing it out as it supports *Prediction 4b*, which states that because adults are more familiar with the surrounding landscapes they are more likely to reach refugia habitats than juveniles.

Despite the fact that a proportion of kites moved from the most to the least-impacted regions, most birds did not appear to successfully reach refugia habitats and overall, this regional drought had a substantial demographic effect on the population (Fig. 2), which is consistent with *Prediction 5a*. The survival analysis conducted over the last 13 years, at the scale of the whole population, also indicates that apparent survival varied among regions. During nondrought, adult survival was lower in northern regions (K and J) than in southern regions (E and O), possibly because of lower apple snail availability in the northern regions (Cattau unpublished). Juvenile apparent survival was also lower in northern regions than in southern regions during nondrought years, but differences were not statistically significant. Our results supported *Prediction 5b*, which predicted that survival should be lower in areas most impacted by the drought than in areas least impacted. Adult apparent survival in regions E, O and J (lowest DSV), decreased significantly during the drought, while survival in K (highest DSV) did not decrease (Fig. 2). *Prediction 5b* could not be tested for juveniles because of low sample size. When averaging survival over all the regions apparent survival of adults decreased by 16% during the drought while juvenile apparent survival

dropped by more than 86% during the drought (Fig. 2). Thus, the drought had a larger effect on juvenile apparent survival than on adult apparent survival, which is consistent with *Prediction 5c.* Interestingly, adult apparent survival only decreased significantly between 2001 and 2002, while juvenile apparent survival had already decreased significantly between 2000 and 2001, indicating that juveniles were also more susceptible to early effects of the drought. A declining trend in juvenile apparent survival is also evident in Fig. 2. However, we had no good a priori reason to expect this trend. It could be due to stochastic variation or unrecognized variations in wetland conditions. Additionally, we should note that of 65 juveniles equipped in 2003 with radio transmitters, 36 were observed alive between March and May 2004 (Martin *et al*. unpublished data). Therefore, juvenile survival between 2003 and 2004 rebounded since the drought to at least 0·55 (detection probability was not accounted for this estimate).

The dry-down effects of the drought began in mid January 2001; most of the birds that fledged during the previous breeding season (from the 2000 cohort) were approximately 9 months. Because juveniles are somewhat proficient at capturing snails after only 2 months (Beissinger 1988), by 9 months these birds should be equally efficient at capturing and extracting snails. Field observations of kite interactions indicate no dominance of adults over juveniles that are 4 months or older (Martin *et al*. unpublished data). The only major difference in foraging abilities between young and older birds, that we are aware of, would be their respective familiarity with the landscapes. Adults would potentially have explored more wetlands than juveniles (Bennetts *et al*. 2002). This may thus explain the weaker effect of the drought on adults (see *Prediction 5c*).

We note that the survival estimates presented in this study are apparent survival estimates, indicating that the complement of these estimates includes both mortality and permanent emigration from the study system. Thus, lower survival during drought could be due to both permanent movement out of the system and lower true survival due to the drought. It is possible that some kites moved temporarily to peripheral habitats (typically highly disturbed habitats: agricultural areas, large canal) during drought. Although these habitats will typically retain more water than major kite habitats during drought, they are unlikely to be suitable for breeding activity; thus, when conditions improve, most birds should move back to major wetlands. Hence, because the snail kite population in Florida is assumed to be an isolated population (Bennetts *et al*. 1999) and because the geographical scope of our study encompasses the major kite habitats, it is unlikely that many kites remained outside the sampled areas for three consecutive sampling seasons after the drought. Even if substantial temporary emigration into unsampled areas occurred during drought it would not have biased survival if it was followed by movement back into the study system when conditions improved.

Conclusions and conservation implications

Reducing habitat fragmentation has now become almost a rubber-stamp recommendation for maintaining populations of many species of terrestrial mammals, insects, and even birds with reduced dispersal abilities. However, the benefits may be less obvious when dealing with species able to cover several hundred kilometres in one day and whose daily dispersal abilities exceed the distance separating patches that have been isolated through fragmentation. As suggested by previous theoretical studies (e.g. Doak, Marino & Kareiva 1992), we found that considering scale issues was critical to understanding movement of kites in fragmented landscapes. The case study of the snail kite in Florida also provides an example of how fragmentation could indirectly affect the persistence of species with great dispersal abilities. As suggested by Bennetts & Kitchens (2000) and Bell (1991), exploratory behaviours may be important for many animals to resist periodic low food availability events (such as droughts). Thus, if fragmentation reduces exploratory movements of kites, it could also reduce resistance of the kite population to disturbance events. Further work to support this hypothesis may be particularly critical to conserve this endangered species, but may also be relevant to other avian nomads (e.g. water birds in Australia, see Roshier *et al*. 2001).

References

Beissinger, S.R. (1986) Demography, environmental uncertainty, and the evolution of mate desertion in the snail kite. *Ecology*, **67**, 1445–1459.

Beissinger, S.R. (1988) The snail kite. *Handbook of North American Birds* (ed. R.S. Palmer), Vol. IV, pp. 148–165. Yale University Press, New Haven, CT.

Beissinger, S.R. (1995) Modelling extinction in periodic environments: Everglades water levels and snail kite population viability. *Ecological Applications*, **5**, 618–631.

Beissinger, S.R. & Takekawa, J.E. (1983) Habitat use by and dispersal of snail kites in Florida during drought conditions. *Florida Field Naturalist*, **11**, 89–106.

Bell, W.J. (1991) *Searching Behavior: the Behavioral Ecology of Finding Resources*. Chapman & Hall, Cambridge.

Bennetts, R.E. (1998) The demography and movements of snail kites in Florida. PhD Thesis, University of Florida, Gainesville.

Bennetts, R.E. & Kitchens, W.M. (2000) Factors influencing movement probabilities of a nomadic food specialist: proximate foraging benefits or ultimate gains from exploration? *Oikos*, **91**, 459–467.

Bennetts, R.E., Dreitz, V.J., Kitchens, W.M., Hines, J.E. & Nichols, J.D. (1999) Annual survival of snail kites in Florida: radio telemetry versus capture-resighting data. *Auk*, **116**, 435–447.

Bennetts, R.E., Kitchens, W.M. & Dreitz, V.J. (2002) Influence of an extreme high-water event on survival, reproduction, and distribution of snail kites in Florida. *Wetlands*, **22**, 366–373.

Blums, P., Nichols, J.D., Hines, J.E., Lindberg, M.S. & Mednis, A. (2003) Estimating natal dispersal movement rates of female European ducks with multistate modelling. *Journal of Animal Ecology*, **72**, 1027–1042.

Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Inference: a Practical Information-Theoretic Approach*. Springer-Verlag, New York.

Burnham, K.P., Anderson, D.R., White, G.C., Brownie, C. & Pollock, K.H. (1987) *Design and Analysis of Methods for Fish Survival Experiments Based on Release-Recapture*. American Fisheries Society Monograph. American Fisheries Society, Bethesda, MD.

Cam, E., Oro, D., Pradel, R. & Jimenez, J. (2004) Assessment of hypotheses about dispersal in a long-lived seabird using multistate capture–recapture models. *Journal of Animal Ecology*, **73**, 723–736.

Choquet, R., Reboulet, A.M., Pradel, R., Gimenez, O. & Lebreton, J.-D. (2003) *User's Manual for U-Care, Utilities–Capture–recapture, V2·02*. CEFE/CNRS, Montpellier (ftep://ftp.cefe.cnrs-mop.fr/biom/U-CARE).

Clobert, J., Dhont, A.A., Danchin, E. & Nichols, J.D., eds. (2001) *Dispersed*. Oxford University Press, Oxford.

Cooch, E.G. & White, G.C. (2005) MARK – an introductory guide. URL: http://phidot.org/software/docs/book

Darby, P.C. (1998) Florida apple snail (*Pomacea paludosa*) life history in the context of a hydrologically fluctuating environment. PhD Thesis, University of Florida, Gainesville.

Davis, S. & Ogden, J. (1994) Toward ecosystem restoration. *Everglades, the Ecosystem and its Restoration* (eds J.C. Ogden & S.M. Davis), pp. 769–796. St Lucie Press, Delray Beach, FL.

DeAngelis, D.L. & White, P.S. (1994) Ecosystems as products of spatially and temporally varying driving forces, ecological processes and landscapes: a theoretical perspective. *Everglades, the Ecosystems and its Restoration* (eds J.C. Ogden & S.M. Davis), pp. 9–27. St Lucie Press, Delray Beach, FL.

DeLaune, M.G. (2000) *Xtools Arcview Extension* Version 9/15/03. URL: *http://www.odf.state.or.us/divisions/management/State_forests/XTools.asp*

Doak, D.F., Marino, P.C. & Kareiva, P.M. (1992) Spatial scale mediates the influence of habitat fragmentation on dispersal success. Implication for conservation. *Theoretical Population Biology*, **41**, 315–336.

Haddad, N.M. (1999) Corridor and distance effects on inter-patch movements: a landscape experiment with butterflies. *Ecological Applications*, **9**, 612–622. 34.

Hanski, I. (1999) *Metapopulation Ecology*. Oxford University Press, Oxford.

Hanski, I. (2001) Population dynamics consequences of dispersal in local populations and in metapopulations. *Dispersal* (eds J. Clobert, A.A. Dhont, E. Danchin & J.D. Nichols), pp. 283–298. Oxford University Press, Oxford.

Hestbeck, J.B., Nichols, J.D. & Malecki, R.A. (1991) Estimates of movement and site fidelity using mark-resight data of wintering Canada geese. *Ecology*, **72**, 523–533.

Holt, R.D. & Debinski, D.M. (2003) Reflections on landscapes experiments and ecological theory: tools for the study of habitat fragmentation. *How Landscape Change* (eds G.A. Bradshaw & P.A. Marquet). Springer-Verlag, Berlin.

Kitchens, W.M., Bennetts, R.E. & DeAngelis, D.L. (2002) Linkages between the snail kite population and the wetland dynamics in a highly fragmented South Florida Hydroscape. *The Everglades, Florida Bay, and Coral Reefs of the Florida Keys* (eds J.W. Porter & K.G. Porter), pp. 183–203. CRC Press, Boca Raton, FL.

Light, S.S. & Dineen, J.W. (1994) Water control in the Everglades: a historical perspective. *Everglades, the Ecosystem and its Restoration* (eds J.C. Ogden & S.M. Davis), pp. 47–84. St Lucie Press, Delray Beach, FL.

Lomolino, M.V. (1990) The target area hypothesis: the influence of island area on immigration rates of non volant mammals. *Oikos*, **57**, 297–300.

Pradel, R., Wintrebert, C.M.A. & Gimenez, O. (2003) A proposal for a Goodness-of-Fit test to the Arnason-Schwarz multisite capture–recapture model. *Biometrics*, **59**, 43–53.

Roshier, D.A., Robertson, A.I., Kingsford, R.T. & Green, D.G. (2001) Continental–scale interactions with temporary resources may explain the paradox of large populations of desert waterbirds in Australia. *Landscape Ecology*, **16**, 547–556.

Schtickzelle, N. & Baguette, M. (2003) Behavioral responses to habitat patch boundaries restrict dispersal and generate emigration-patch area relationships in fragmented landscapes. *Journal of Animal Ecology*, **72**, 533–545.

Senar, J.-C., Conroy, M.J. & Borras, A. (2002) Asymmetric exchange between populations differing in habitat quality: a metapopulation study on the citril finch. *Journal of Applied Statistics*, **29**, 425–441.

Smith, J.N.M. & Hellmann, J.J. (2002) Population persistence in fragmented landscapes. *Trends in Ecology and Evolution*, **17**, 397–399.

Smith, S.M., Gawlik, D.E., Rutchey, R., Crozier, G.E. & Gray, S. (2003) Assessing drought-related ecological risk in the Florida Everglades. *Journal of Environmental Management*, **68**, 355–366.

Stamps, J.A. (2001) Habitat selection by dispersers: integrating proximate and ultimate approaches. *Dispersal* (eds J. Clobert, E. Danchin, A.A. Dhont & J.D. Nichols), pp. 230–242. Oxford University Press, Oxford.

Takekawa, J.E. & Beissinger, S.R. (1989) Cyclic drought, dispersal and conservation of the snail kite in Florida: lessons in critical habitat. *Conservation Biology*, **3**, 302–311.

White, G.C. & Burnham, K.P. (1999) Program MARK: Survival rate estimation from both live and dead encounters. *Bird Study*, **46** (Suppl.), S120–S139.

Williams, B.K., Nichols, J.D. & Conroy, M.J. (2002) *Analysis and Management of Animal Populations*. Academic Press, San Diego.

Supplementary material

Appendix S1. Method from Burnham *et al.* (1987) to compute confidence intervals.

Table S2. Multistate models of monthly movement probabilities (ψ) of adult (*ad*) and juvenile (*juv*) snail kites among the five major regional patches in Florida based on radio-telemetry data.

Table S3. Multistate models (with survival and detection probabilities equal to 1) of monthly movement probabilities (ψ) of adult (*ad*) and juvenile (*juv*) snail

kites among wetlands in the E and K region based on radio-telemetry data.

Table S4. Multistate models of annual survival (ϕ), sighting probabilities (p), and annual movement probabilities (ψ) of adults (*ad*) and juveniles (*juv*) snail kites based on banding data.

Table S5. Annual movement estimates ($\hat{\psi}$), between the 4 major regions used by the snail kite (E, O, K and J) during normal and drought years estimated using the most parsimonious model in Table 3.

© 2006 The Authors.
Journal compilation
© 2006 British
Ecological Society,
*Journal of Animal
Ecology*, **75**,
527–539